Jl S. Afr. Bot. 46 (1): 67–88 (1980)

THE GENUS *EUGENIA* L. (MYRTACEAE) IN SOUTHERN AFRICA: 1. THE NATURE AND TAXONOMIC VALUE OF THE FIRST-FORMED STEM PERIDERM*

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Abstract

The nature of the first-formed stem periderm of some *Eugenia* species of Southern Africa was examined. Both the quantitative and qualitative characteristics of this tissue were evaluated for their taxonomic importance. This was done on the basis of a review of the known taxonomic value of the periderm with special reference to its application in the Myrtaceae.

A number of periderm characteristics were found which support the division of the species into two distinct groups. The most important of these is the position in which the periderm originates in the stem. From this it can be concluded that the first-formed stem periderm initiates either in the cortex (Group X) or in the primary external phloem (Group Y). This characteristic is correlated with two structurally different types of phellem and proves to be constant for a species. The identity of species with a hitherto vague taxonomic position, could be ascertained by checking the position in which the periderm originates in the type specimens.

The grouping of specimens based on periderm characteristics, closely agrees with the revision of Dümmer (1912). It does, however, not support the delimitation of some of the taxa as proposed by White (1977) in the most recent revision of the genus *Eugenia* in Southern Africa.

Uittreksel

DIE GENUS *EUGENIA* L. (MYRTACEAE) IN SUIDELIKE AFRIKA: 1. DIE AARD EN TAKSONOMIESE BETEKENIS VAN DIE EERSTE GEVORMDE STINGELPERIDERM

Die aard van die eerste gevormde stingelperiderm van 'n aantal *Eugenia*-spesies uit Suidelike Afrika is ondersoek. Beide kwantitatiewe en kwalitatiewe kenmerke van hierdie weefsel is vir hul taksonomiese waarde geëvalueer. Dit is gedoen in die lig van 'n oorsig van die reeds bekende taksonomiese waarde van die periderm met besondere verwysing na die toepassing daarvan in die Myrtaceae.

'n Aantal peridermkenmerke wat die verdeling van die spesies in twee verskillende groepe ondersteun, is gevind. Die belangrikste hiervan is die posisie in die stingel waar die

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* This paper is based on results included in a thesis submitted by the first author to the Department of Botany, Potchefstroom University for C.H.E., in partial fulfilment of the requirements for the degree Magister Scientiae.

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Accepted for publication 16th March 1979.

periderm ontstaan. Hiervolgens kan die eerste gevormde stingelperiderm òf in die korteks (Groep X) òf in die primêre eksterne floëem (Groep Y) ontstaan. Hierdie kenmerk is met twee struktureel-verskillende tipes felleem gekorreleer en blyk konstant te wees vir 'n spesie.

Deur die posisie van peridermvorming by die tipe-eksemplare te kontroleer, kon die identiteit van spesies waarvan die taksonomiese posisie tot nog toe vaag was, vasgestel word.

Daar is gevind dat die groepering van eksemplare volgens peridermkenmerke nou ooreenstem met die hersiening van Dümmer (1912), maar nie die omgrensing van sommige taksons soos voorgestel in die jongste hersiening van die genus *Eugenia* in Suidelike Afrika (White, 1977), ondersteun nie.

1. INTRODUCTION

The genus *Eugenia* L. is one of the largest woody genera in the world (Good, 1969) and taxonomically one of the most difficult taxa to deal with. There are few other genera that confront the taxonomist with so many problems. One of these is the lack of useful and reliable external morphological characteristics which may be used to distinguish between the hundreds of described species.

This is also the case with the *Eugenia* species of Southern Africa where many herbarium specimens cannot be identified.

As an introduction to a revision of *Eugenia* in Southern Africa, an anatomical study of the leaf and stem has been undertaken (Van Wyk, 1978). One of the objectives was to evaluate a number of anatomical characteristics as an aid to the identification of taxa and to use such diagnostic characteristics to determine the identity of hitherto vaguely known species. It is the aim of this paper to describe and evaluate some characteristics of the first-formed periderm in the stem, and to discuss some of its taxonomic implications. Before evaluating the periderm characteristics it is necessary to briefly review the known taxonomic value of this tissue with special reference to its application in the Myrtaceae.

In comparative anatomical studies characteristics of the bark or rhytidome rather than only those of the periderm, are usually used. Despite the diagnostic appearance of the external surface pattern of the bark of many woody plants, not much effort has been made to correlate it with the internal structure (Whitmore, 1962 (a), (b) and (c)). The work of Douliot (1889) according to Carlquist (1961) nevertheless already contains systematically arranged information on the site of periderm initiation for a large number of genera. In a revision of the genus *Eugenia* s.l. in Malaya, Henderson (1949) stressed the large diagnostic value that the bark of this genus possess in field studies.

According to Lignier (1887, 1890) the phellem of the Myrtaceae consists of layers of radially flattened cells with thin or sclerified walls alternating with radially elongated thin-walled cells. The cell walls of the radially flattened cells are not suberised and are known as phelloids (Esau, 1965). Van Tieghem (1904) according to Solereder (1908) showed that the cell-shape of the different layers can also be the reverse of Lignier's results. Phellem consisting only of cubical thin-walled cells occurs in some species of *Eucalyptus* and *Syzygium* (Metcalfe & Chalk, 1965).

The first-formed periderm in the stem of the Myrtaceae usually either originates in the parenchyma cells of the cortex or in the primary external phloem to the inside of the extraxylery ring of fibres (Blyth, 1958)—also called the pericycle (Lignier, 1887; Metcalfe & Chalk, 1965). According to Lignier (1887) the method of decortification is one of the more constant stem characteristics of the Myrtaceae that can be used for the purpose of identification. Although this characteristic is of value for the recognition of genera and subgenera (Solereder, 1908) it is important to bear in mind that the first-formed periderm is always more superficial than successive periderms (Metcalfe & Chalk, 1965). Metcalfe and Chalk (1965) also question the taxonomic value of the exact position in which the periderm originates (e.g. superficial or deep in the cortex). For the genus *Eugenia* the position in which the periderm originates can vary according to the species (Metcalfe & Chalk, 1965).

As examples of bark studies in the Myrtaceae the works of Brögli (1926) on *Eucalyptus* and *Eugenia* and Chattaway (1955 (a), (b), (c), 1959) on *Eucalyptus,* deserve mentioning. Chattaway (1953) found that the first-formed periderm coincides to a large extent in more than 150 *Eucalyptus* species. The nature of the rhytidome, however, was taxonomically important and could be used for the identification of species in which external morphological features show great similarity. It has further been found that the grouping of species according to bark characteristics supported a reclassification of species based on morphological characteristics.

The division of the *Eugenia* species of the Old and New World into two separate groups on the basis of wood anatomy (Dadswell & Ingle, 1947), is confirmed by the anatomy of the bark (Chattaway, 1959). This division supports the proposed classification of Merrill and Perry (1938 (a), (b), (c), 1939) which is also supported by other characteristics (Pike, 1956; Schmid, 1972).

The many periderm characteristics that can be used in comparative anatomy [Solereder, 1908; Chattaway 1953, 1955 (a) + (b); Carlquist, 1961; Whitmore, 1962 (a)] are usually very constant and are little influenced by external environmental factors. In this regard Bamber (1962) found that the characteristics of the bark of the Leptospermoideae are of greater taxonomic value than those of the wood of the same group.

Little is known about the seasonal activity and control over the initiation of the phellogen (Zimmerman & Brown, 1974). In this connection the work of Waisel, Lipschitz and Arzee (1967) shows that the phellogen can possess a seasonal rhythm that does not necessarily coincide with that of the vascular cambium.

2. Material and Methods

Both dried and preserved material have been used. Material from different localities was selected to determine possible environmentally induced variation. Where possible plants of a particular species from at least five different localities were studied quantitatively to determine intraspecific variation. All material was identified by the first author according to the criteria used by Sonder (1862), Engler (1899), Dümmer (1912), Brown (1912), Engler and von Brehmer (1917), Strey (1972) and Van Wyk (1979).

The species discussed in this paper as well as the number of specimens of each species that were examined are given in Table 1. The names of the collectors and the collectors' numbers for the examined specimens can be found in Van Wyk (1978).

Dried material from herbarium sheets was rehydrated by transferring it to distilled water in which it was slowly heated and then boiled for about 30 minutes. Fresh and rehydrated material were fixed in formalin-acetic acid-alcohol (Johansen, 1940).

Fixed material was dehydrated with an ethanol-*n*-propanol-*n*-butanol series and infiltrated and embedded in a monomer mixture of purified glycol methacrylate or unpurified hydroxyethyl methacrylate (HEMA) (Feder & O'Brien, 1968).

Sections 2–4 μm thick were cut with a glass knife on an ultra-microtome and stained with toluidine blue or with periodic acid—Schijff (PAS) stain with

TABLE 1.

Species and number of specimens examined. (Species are grouped according to the results of the study. An asterisk indicates that type material of the species was also studied anatomically)

Species	Number of specimens examined quantitively	Total number of specimens examined
GROUP X		
**Eugenia capensis* (Eckl. + Zeyh.) Sond.	5	30
**E. gueinzii* Sond.	—	1
E. cf. *mossambicensis* Engl.	4	19
**E. natalitia* Sond.	6	40
**E. rudatisii* Engl.	—	1
**E. simii* Dümmer	3	19
GROUP Y		
**E. albanensis* Sond.	—	20
**E. erythrophylla* Strey	5	22
E. pusilla N.E.Br.	—	1
**E. verdoormae* Van Wyk[1]	5	10
**E. woodii* Dümmer	—	15
**E. zeyheri* Harv.	2	11
**E. zuluensis* Dümmer	3	11

* [1] Previously referred to as *E.* sp. nov. (Van Wyk, 1978).

toluidine blue as a counterstain (Feder & O'Brien, 1968). Schijff's reagent was prepared according to the method in Gurr (1963).

After staining with toluidine blue, sections of material embedded in unpurified HEMA were treated according to the method used by Ruddel (1967).

Freehand sections of fixed material were made to check the constancy of some characteristics for a species. For the localisation of lignified tissue and the periderm the phloroglucinol/hydrochloric acid method was used (Radford, Dickison, Massey & Bell, 1974).

The presence of tannin and suberin was shown with ferrichloride and Sudan IV respectively (Johansen, 1940).

Only transverse sections through the internodes of the stem were made.

Measurements were taken with an eyepiece micrometer. For practical reasons, a maximum of thirty readings per section were made for a specific characteristic. The mean of these readings is often affected by the few very low or high values that may occur. The median is however often a more representative value (Sokal & Rohlf, 1969), and was thus used in this study.

The size and wall thickness of the phellem and phelloid cells were measured as follows:

(a) Phellem cells:
The tangential and radial diameter were respectively measured between the outer edge of the two radial and tangential cell walls of thirty adjacent phellem cells on the same sections. In most cases the first or second row of phellem cells from the phellogen was used. At the same time the maximum thickness of the inner tangential walls was noted.

(b) Phelloid cells:
Measurements were made in the same way as in the case of the phellem cells. Usually the youngest row of phelloids in which the walls of the phelloid cells showed maximum thickness, was used.

Preference was given to those areas on a section where the thickest lignified walls occurred.

3. RESULTS

3.1 *Nature of the periderm*

A periderm is initiated at an early stage in the development of the stem of all the species investigated.

The phellogen and phellem are easy to distinguish, but the phelloderm is poorly developed, usually consisting of a single layer of radially flattened thin-walled cells which are tanniniferous.

The phelloderm shows little variation in all the species and it has not been investigated quantitatively.

The phellem is characteristically that of the Myrtaceae (Metcalfe & Chalk, 1965) and possesses phelloids in which usually only the inner tangential and radial walls are strongly thickened and lignified. As a result the phelloids appear horseshoe-shaped in cross section. These sclerified walls are usually, but not necessarily always, present in all the phelloids. They are particularly poorly developed in the older phelloid layers of *E. zuluensis* (Fig. 16). Lamellae can usually be distinguished in the thickened walls (Fig. 15). Most often a layer of phellem cells alternates with a layer of phelloids. Multiserial phelloid areas, however, are present in parts of the periderm of some specimens (Fig. 8).

Both the phellem cells and phelloids may be filled with tannin (Fig. 9). Radial phellem rays, one or more cells wide, of thin-walled and sclerified cells, are often present in the phellem (Fig. 14).

Although some lenticels were present on a few slides, especially in those of *E. capensis*, their nature and taxonomic value have not been investigated.

Structurally the periderm of the Southern African *Eugenia* species indicates an affinity with the *Eugenia* species of the New World (*Eugenia* s. str.; Chattaway, 1959).

3.2 *Origin of the periderm*

On the basis of the position in which the first periderm originates in the stem, the *Eugenia* species of Southern Africa can be divided into two groups. These two groups will be referred to as Group X and Group Y (Table 1; Fig. 1).

In Group X the phellogen originates in the parenchyma of the cortex, immediately below the epidermis. No decortification occurs as a result of this periderm (Fig. 6).

In Group Y the phellogen originates in the primary external phloem parenchyma, immediately inside the extraxylary ring of fibres (pericycle) (Figs 11 and 12). The cortex and epidermis shrivel shortly after the formation of the first layer of phellem cells and are pushed off together with the fibre ring (Fig. 13). Especially in freehand sections, older secondary phloem can be confused with the cortex because of the absence of the fibre ring in some specimens. However, secretory cavities are characteristically present in the cortex, but absent from the secondary phloem.

In order to determine the constancy of this characteristic, a number of specimens of most species have been investigated. Where possible, material obtained from the type specimens has been included. From these results it appears that the position in which the periderm initiates in normal stems is constant for a species.

In the same stem, under abnormal conditions, the phellogen can develop in two different positions (Fig. 10). This has been recorded in a specimen of Group X in which part of the superficial layers of the cortex was damaged. In

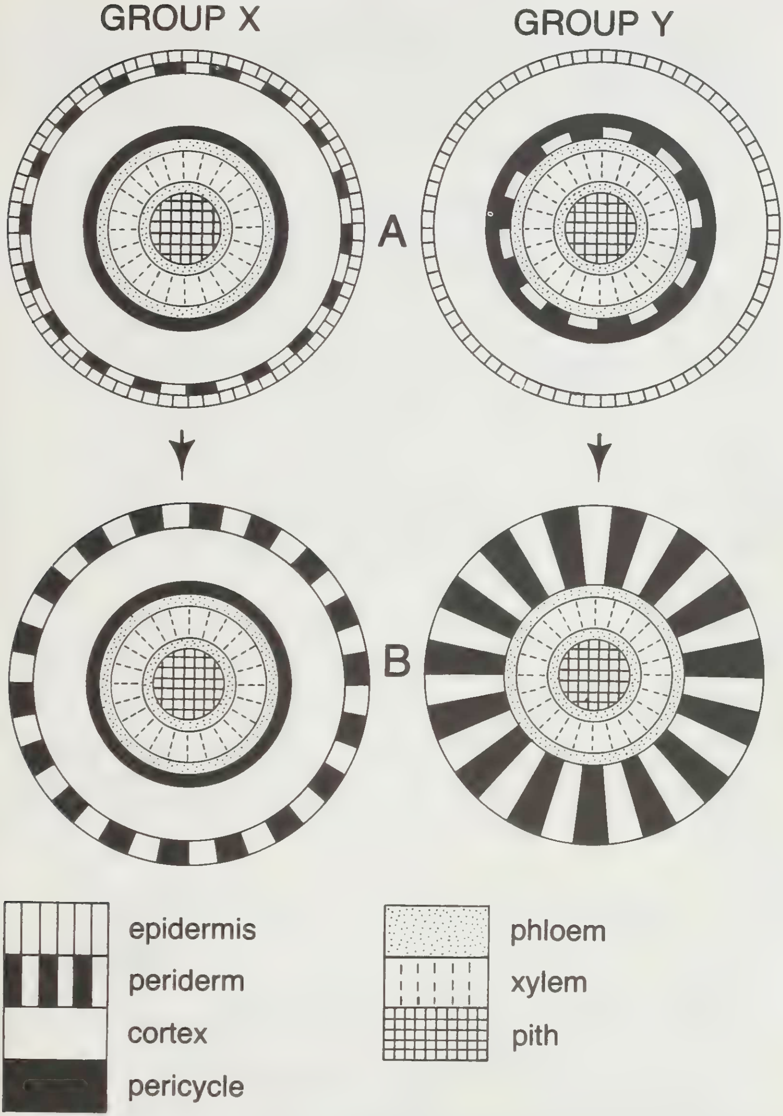

Fig. 1.

Line drawings of stems in transverse section to show the position of the periderm and distribution of the principle tissues in the two species groups which are distinguished. Group X = Periderm superficial in cortex. Group Y = Periderm in primary external phloem. A: Young stem; B: Older stem.

this specimen the periderm is continuous and develops partly subepidermally in the cortex and partly in the primary external phloem—the latter part opposite the damaged cortex.

3.3 *Nature of the cells in the phellem*

3.3.1 Phelloids

In Fig. 2 a scatter diagram is used to correlate the median of the tangential diameter of the phelloids with the median of their radial diameter. From this diagram it seems that the *Eugenia* species can be

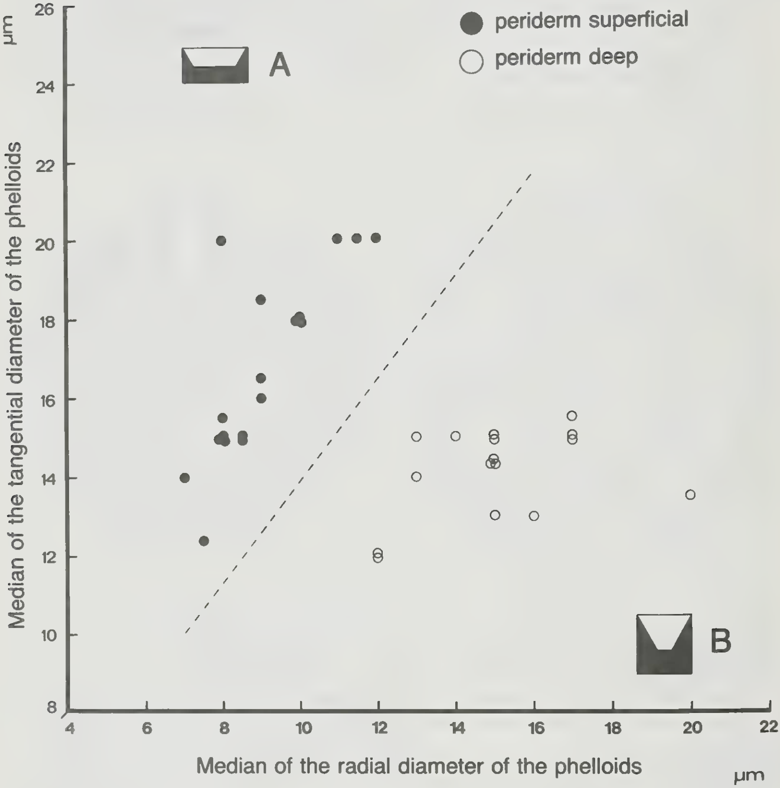

Fig. 2.

Scatter diagram to correlate the radial and tangential diameter of the phelloids. The schematic presentation of the phelloids (A + B) is according to scale and based on the mean of all the median values.

divided into two groups. This division correlates with the position in which the periderm originates. Species belonging to Group X possess phelloids which are radially flattened (Figs 7 and 8) while those of Group Y are radially elongated (Figs 14 and 15). The inner tangential cell walls of Group X are also more thickened than those of Group Y (Figs 7, 8, 14 and 15).

It is further noticeable that the thickened cell walls of Group X are more persistent than those of Group Y. Cell walls of the last mentioned group are often already delignified, or in a state of disintegration in the third phelloid layer from the phellogen (Fig. 15).

Numerous pits are present in the lignified walls of Group X (Fig. 9), while in Group Y they are usually poorly developed (Fig. 15). Lignified cell walls in sections stained with PAS/toluidine blue turned dark red in the case of Group Y but stained lightly in Group X. This may indicate possible differences in the chemical composition of the walls.

The size and wall thickness of the phelloids show little interspecific variation.

The mean of the cell diameter and wall thickness of the median values of the various observations has been separately calculated for all the specimens of Group X and Y and is shown in Table 2.

TABLE 2.
Size of the phelloids. (The mean and standard deviation of the values used in Fig. 2 & Fig. 4)

	Group X	Group Y
Tangential diameter	17,03 ± 2,15 μm	14,16 ± 1,12 μm
Radial diameter	9,15 ± 1,40 μm	15,06 ± 2,09 μm
Thickness of inner tangential walls	3,76 ± 0,90 μm	5,96 ± 2,23 μm

3.3.2 Phellem cells

According to Fig. 3 it seems that the size of the phellem cells also supports the division of the *Eugenia* species into two groups.

Phellem cells of Group Y are radially flattened, while in Group X they are radially elongated. The median value of the tangential diameter is much the same in both groups. No prominent interspecific differences were noted.

The cell walls of Group X are slightly thicker than those of Group Y.

The values in Table 3 represent the mean cell size and wall thickness calculated from the median values of all the different measurements for all the specimens of Group X and Y.

TABLE 3.
Size of the phellem cells. (The mean and standard deviation of the values used in Fig. 2 & Fig. 3)

	Group X	Group Y
Tangential diameter	16,68 ± 2,84 μm	14,83 ± 1,74 μm
Radial diameter	16,65 ± 3,04 μm	9,20 ± 1,47 μm
Thickness of walls	1,41 ± 0,48 μm	1,0 ± 0 μm

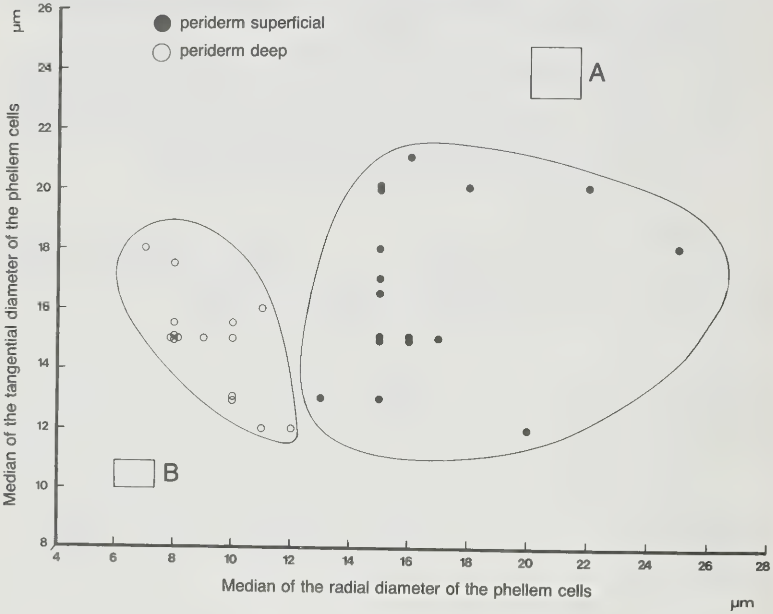

FIG. 3.
Scatter diagram to correlate the radial and tangential diameter of the phellem cells. The schematic presentation of the phellem cells (A + B) is according to scale and based on the mean of all the median values.

3.3 *Structure of the phellem*

The radial diameter of the phellem cells and phelloids is shown by means of a scatter diagram in Fig. 4.

In Group X layers of radially elongated phellem cells alternate with layers of radially flattened phelloid cells. The reverse applies to Group Y. The phellem structure is schematically shown in Fig. 5.

The two different positions in which the periderm originates are thus both correlated with a peculiar structural type of phellem (Figs 7, 8, 14 and 15).

4. DISCUSSION

From a practical viewpoint the position in which the periderm originates is of great taxonomic significance. This characteristic has been investigated in a large number of specimens and was constant for a species. By checking this characteristic in the type specimens the identity of species with hitherto vague taxonomic

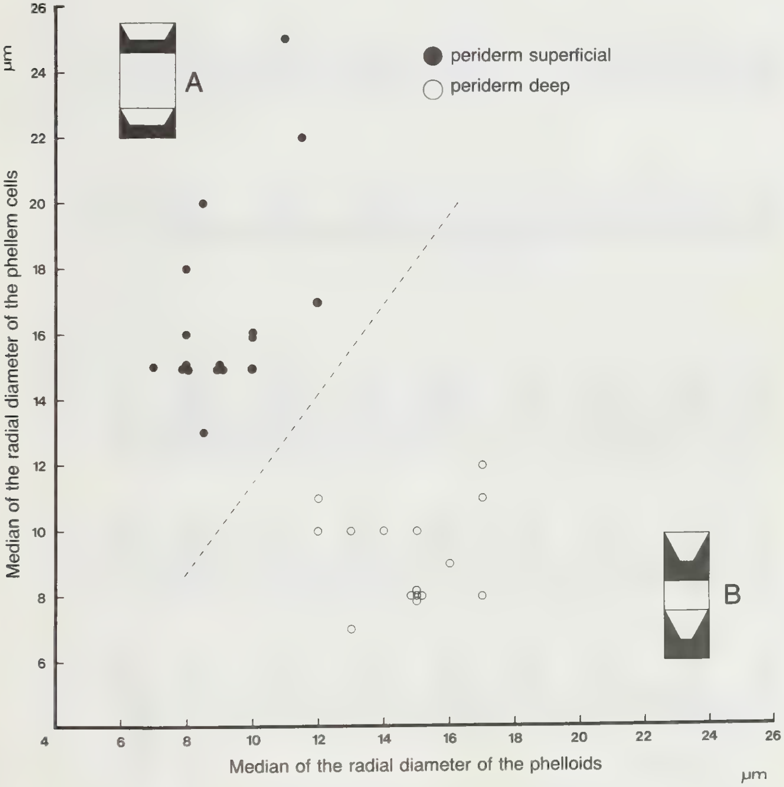

FIG. 4.

Scatter diagram to correlate the radial diameter of the phellem cells with the radial diameter of the phelloids. The schematic presentation of parts of the phellem (A + B) are according to scale and based on the mean of all the median values.

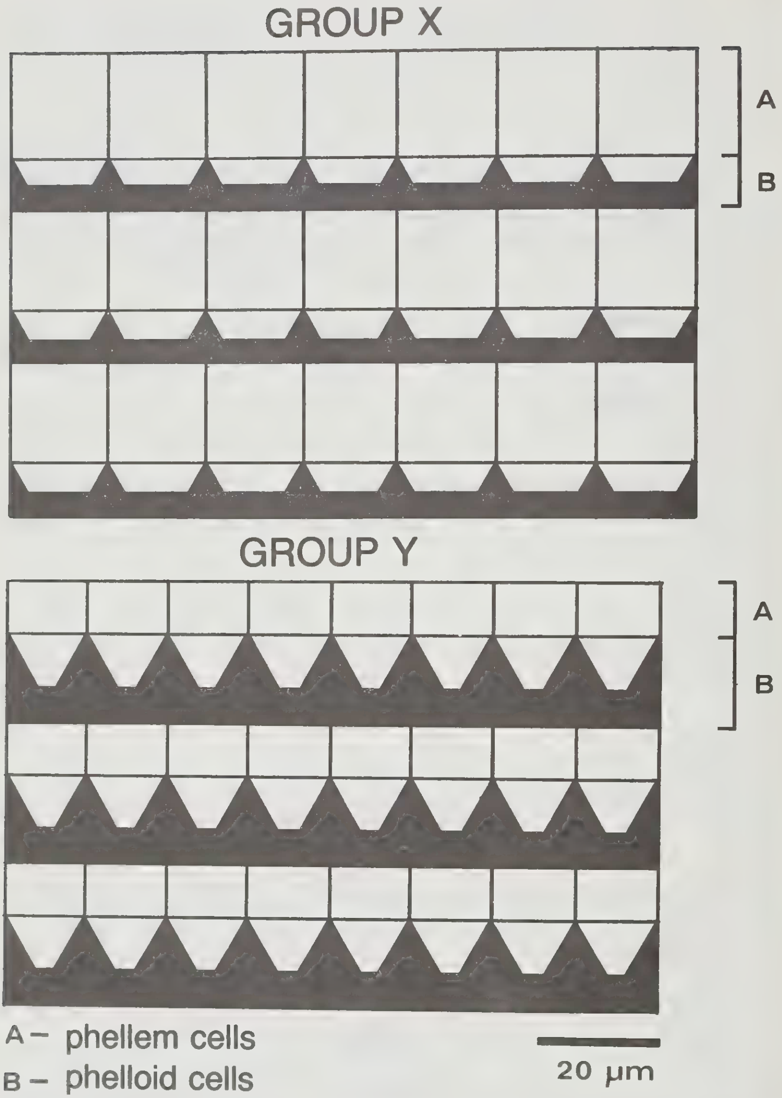

FIG. 5.
Schematic presentation of the structure of the phellem of the first-formed stem periderm in the two species groups; based on the mean values in Tables 2 and 3.

position could be determined. As an example the delimitation of some of the taxa proposed by Dümmer (1912) and White (1977) will next be discussed (Table 4). Taxa which, according to their periderm, belong to Group Y are in CAPITAL letters.

TABLE 4.

A comparison between the treatment of some Southern African *Eugenia* species by different authors. (Taxa belonging to Group Y are in CAPITALS)

Dümmer (1912)	White (1977)
Eugenia capensis (Eckl. + Zeyh.) Sond.	*E. capensis* subsp. *capensis* = *E. capensis*
E. natalitia Sond.	*E. capensis* subsp. *natalitia* (Sond.) F. White = *E. natalitia*
E. WOODII Dümmer	= *E. WOODII*
E. ZULUENSIS Dümmer	= *E. ZULUENSIS*
E. simii Dümmer	*E. capensis* subsp. *simii* (Dümmer) F. White = *E. simii*
E. ZEYHERI Harv.	*E. capensis* subsp. *ZEYHERI* (Harv.) F. White = *E. ZEYHERI*
E. ALBANENSIS Sond.	*E. capensis* subsp. *ALBANENSIS* (Sond.) F. White = *E. ALBANENSIS*
The brackets indicate that *E. simii* and *E. WOODII* have since the revision been confused with *E. ZEYHERI* and *E. natalitia* respectively.	This is a list of only some of the proposed new name combinations and their synonyms. Some of the taxa are described in Coates Palgrave (1977) and White (1978).

After the type material of all the species of Dümmer mentioned in Table 4 have been anatomically investigated the following conclusions with regard to the two classifications can be made.

Dümmer proves to be correct in his distinction of *E. natalitia* (Group X) and *E. WOODII* (Group Y) as two separate taxa. Such is also the case with *E. simii* and *E. ZEYHERI* which belong to two different groups.

According to White (1977) *E. ZULUENSIS* and *E. WOODII* are synonyms of *E. capensis* subsp. *natalitia* (=*E. natalitia*).

This is contradicted by the periderm study according to which the first two species belong to Group Y, while *E. natalitia* belongs to Group X.

With regard to the subspecies of *E. capensis* distinguished by White, it is possible that *E. simii* and *E. natalitia* should be allocated subspecific ranks. However, according to the periderm results, *E. ALBANENSIS* and *E. ZEYHERI* belong to Group Y and cannot be treated as subspecies of *E. capensis* (Group X).

If these two species are in fact of subspecific rank, it must be from a species in Group Y.

The above examples illustrate the practical value of the observed periderm characteristics. These characteristics are in fact supported by some other anatomical and morphological characteristics.

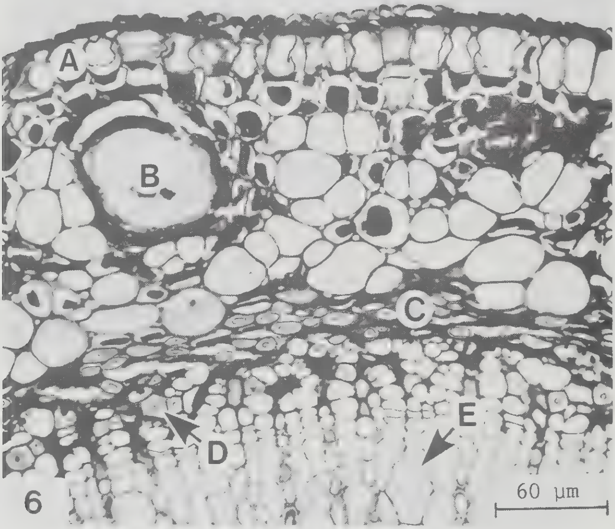

FIG. 6.
Transverse section of the stem of *E. natalitia* to illustrate the periderm (A) which is initiated subepidermally in the cortex; (B) secretory cavity; (C) pericycle with fibres; (D) sclereids in external phloem; (E) crystal bearing idioblast in secondary xylem.

5. CONCLUSIONS

The most important differences between the first-formed stem periderm of Group X and Y are summarised in Table 5. By using the phloroglucinol/hydrochloric acid test on freehand sections of fresh or rehydrated material the nature of the periderm can be ascertained in a quick and easy way. In the herbarium this method is indispensable in order to distinguish between species such as *E. simii* and *E. zeyheri* as well as *E. natalitia* and *E. woodii* which were confused in the past.

It is recommended that the nature of the periderm (especially position in which it is initiated) be investigated for all other members of the genus *Eugenia*. This might prove to be a considerable aid in the identification of specimens which are otherwise often confused.

TABLE 5.

A summary of the expression of some periderm characteristics in the two species groups which are distinguished.

Characteristics	Group X	Group Y
1. Periderm position	superficial in cortex	primary external phloem
2. Phellem cells	radially elongated	radially flattened
3. Phelloids	radially flattened	radially elongated
4. Phelloid walls	3,76 ± 0,9 μm thick	5,96 ± 2,23 μm thick
5. Pits in phelloid walls	numerous	few
6. Nature of thickened walls	relative stable	disintegrate soon after sclerification
7. Thickened walls stained with PAS/toluidine blue	stain dark red	show little staining

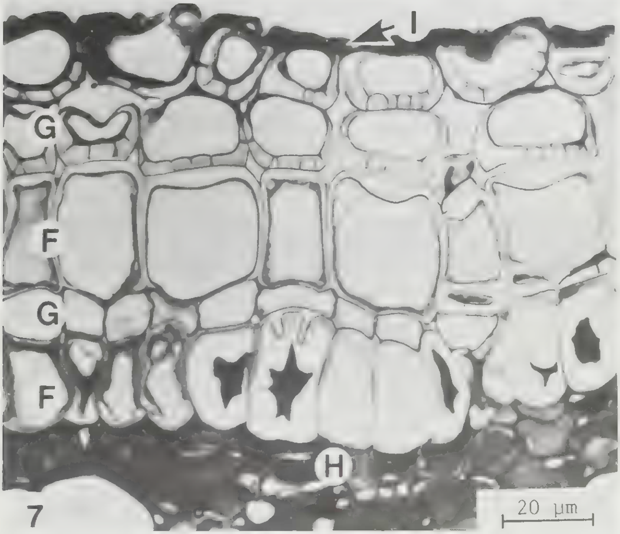

FIG. 7.

Transverse section of the stem of *E.* cf. *mossambicensis* to show the structure of the periderm. (F) radially elongated phellem cells; (G) radially flattened phelloid cells with thickened walls; (H) phellogen; (I) epidermis.

6. ACKNOWLEDGEMENTS

The authors wishes to thank the Director and Staff of the Botanical Research Institute in Pretoria for assistance provided in various ways. The financial aid received from the South African C.S.I.R. is acknowledged with thanks.

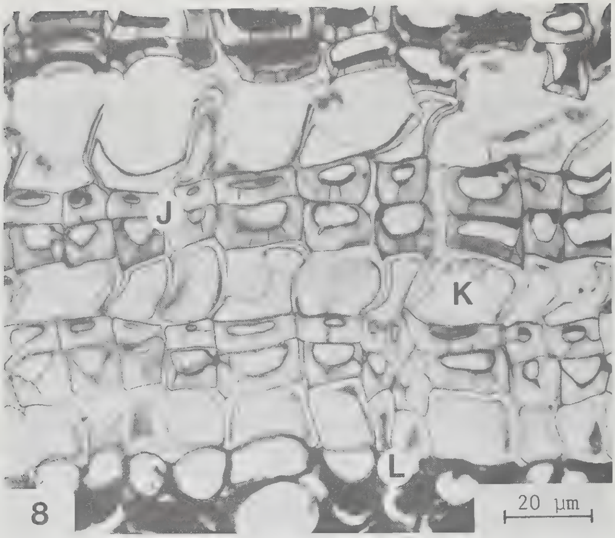

FIG. 8.
Structure of the stem periderm of *E. capensis* as seen in transverse section. Two layers of phelloids (J) alternate with single layers of phellem cells (K). (L) phellogen.

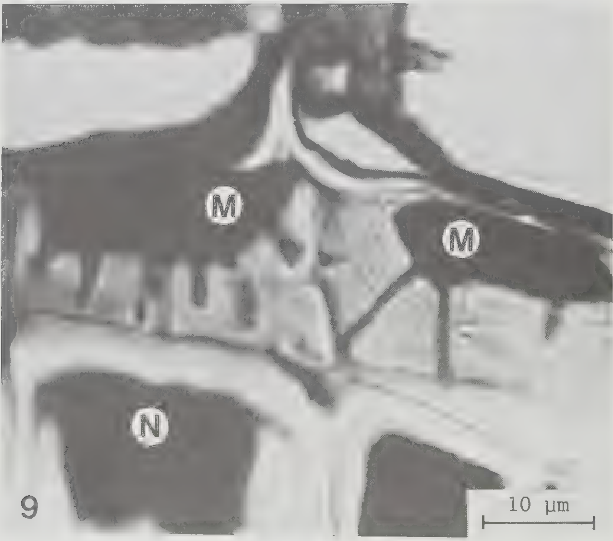

FIG. 9.
Transverse section of the stem periderm of *E. natalitia* to show the numerous pits in the thickened walls of the phelloids (M) which are tanniniferous. (N) phellem cell.

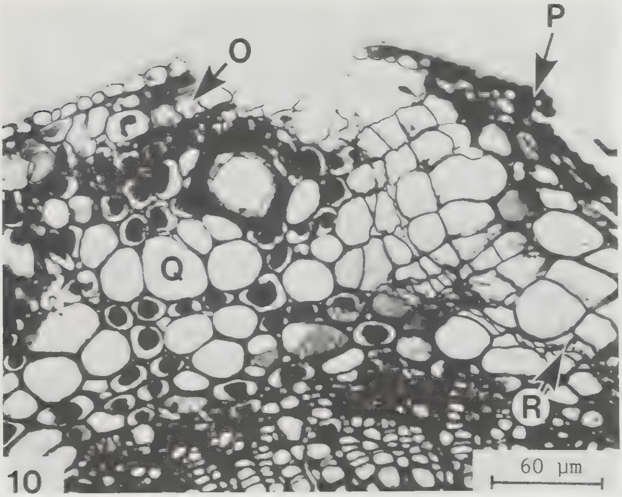

FIG. 10.
Transverse section of the stem of *E. natalitia* to show the superficial phellogen (O) which develops also in the primary external phloem (R) and deeper layers of the cortex (Q) if the superficial cell layers of the stem are damaged (P).

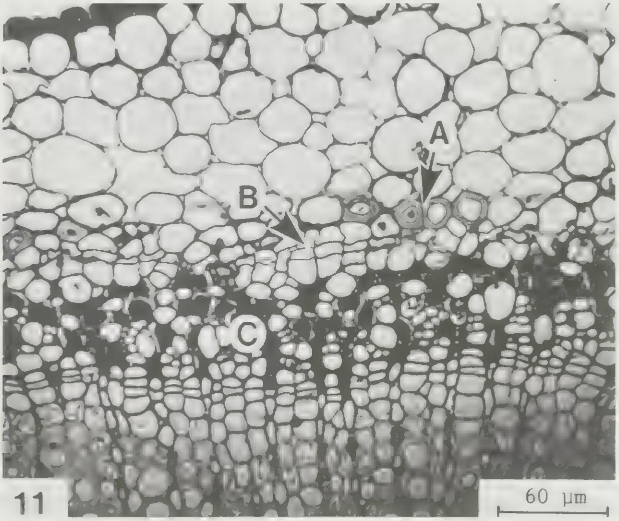

FIG. 11.
Transverse section of the stem of *E. albanensis* to show the initiation of the phellogen (B) in the primary external phloem inside the extraxylary fibre ring (A). (C) secondary external phloem.

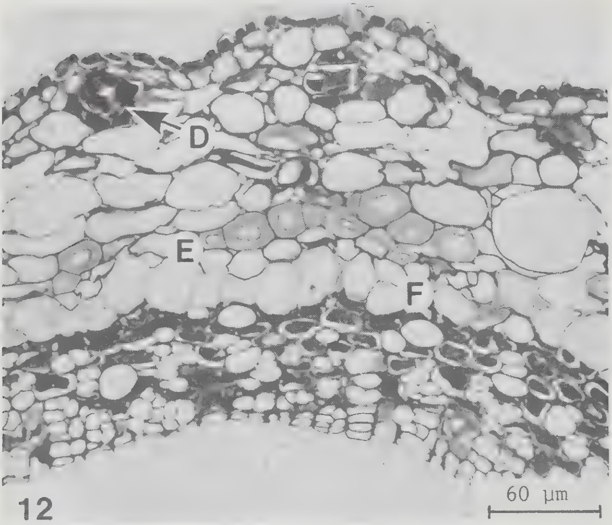

FIG. 12.
Transverse section of an older stem than in Fig. 11 of *E. albanensis* to illustrate the deep seated periderm (F). (E) extraxylary fibre ring; (D) secretory cavity in the cortex.

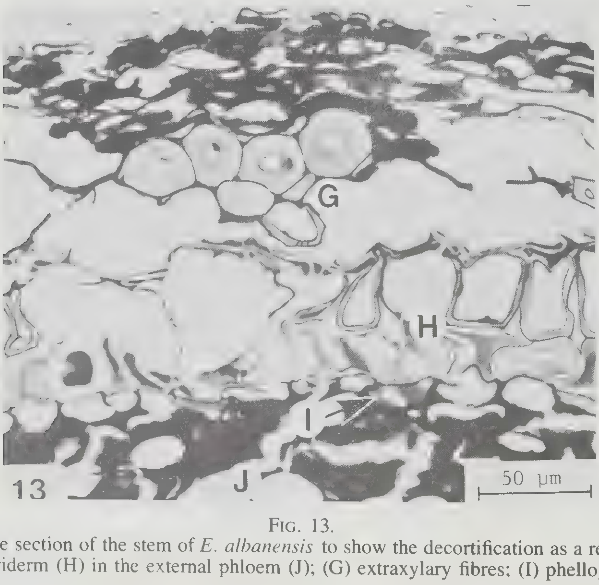

FIG. 13.
Transverse section of the stem of *E. albanensis* to show the decortification as a result of the periderm (H) in the external phloem (J); (G) extraxylary fibres; (I) phellogen.

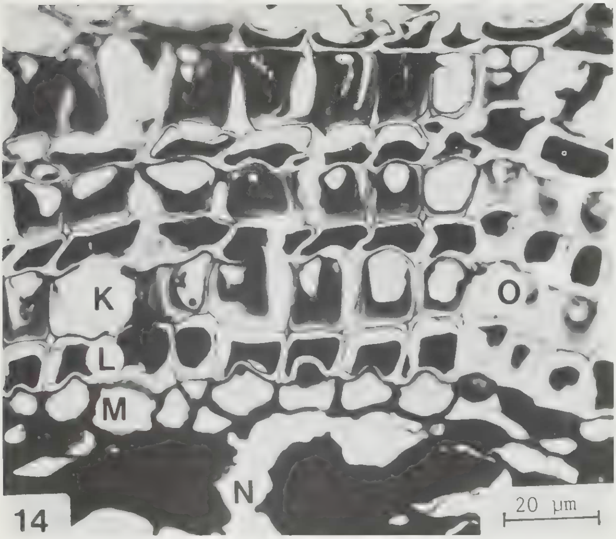

FIG. 14.

Transverse section of the stem periderm of *E. verdoorniae* to illustrate the structure of the periderm. (K) radially elongated phelloids; (L) radially flattened phellem cells; (O) phellem ray; (M) phellogen; (N) secondary external phloem.

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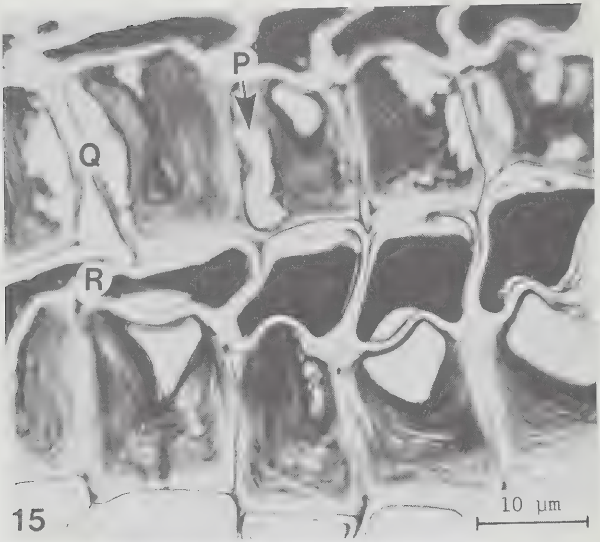

Fig. 15.

Transverse section of the phellem of *E. verdoorniae* to show the layering of the thickened phelloid (Q) walls. These walls disintegrate (P) in older phelloids and show no prominent pits. (R) layer of phellum cells.

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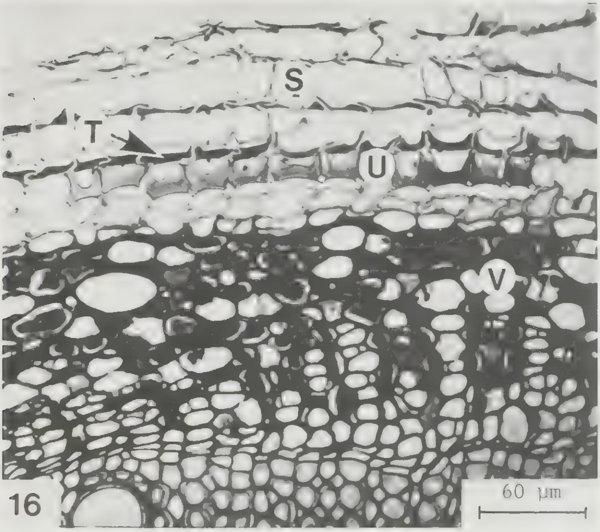

FIG. 16.
Transverse section of the stem of *E. zuluensis*. Note the absence of thickened cell walls in the older phelloid layers (S) and presence in the younger layer (U). (T) phellem cell layer; (V) external phloem.

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